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Taxonomic, functional, and phylogenetic diversity of communities hosting *Ionopsidium savianum* (Brassicaceae) growing on serpentine and limestone substrates

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Abstract

We analysed two different plant communities hosting *Ionopsidium savianum* (Brassicaceae), a species of EU interest included in the Habitats Directive 92/43/CEE annexes, for which specific studies on the ecology of communities where the species grows are lacking and more in-depth knowledge is needed. We examined two important sites of occurrence of this species in Tuscany with different soil types, namely limestone (Mt. Calvi) and serpentine (Mt. Pelato), to determine the structural and functional profile of the communities hosting this species in such different contexts. At each site, we surveyed the plant communities with *I. savianum* in ten 1 m^2 quadrats to determine information on communities' species composition and total plant cover, as well as taxonomic (species richness, and Shannon H' index), phylogenetic (phylogenetic diversity, mean nearest taxon distance and mean pairwise distance) and functional diversity (focusing on Rao's Q, leaf functional traits and adaptive strategies community weighted mean). We took into account site location, soil type, slope aspect and microrelief as plot-level environmental factors. The two communities were highly diverging from multiple points of view. Differences were in species composition, richness and diversity, with Mt. Calvi hosting higher diversity. The indices of phylogenetic diversity were influenced significantly by site and microrelief, allowing the presence of peculiar niches occupied by the fern *Asplenium ceterach*. From the functional point of view, communities at Mt. Calvi showed a higher functional diversity and a higher specific leaf area. Plant height was influenced by the slope aspect and was higher on north-facing slopes. In terms of Grime's adaptive strategies, the Mt. Pelato communities resulted to be more stress tolerant than those surveyed at Mt. Calvi. Here, a decrease in stress-tolerant strategy associated with an increase in ruderal strategy was detected in communities on north-facing slopes.

Keywords

Assembly rules, community ecology, CSR plant strategy, plant traits, serpentine soils, phylogeny

Introduction

Ionopsidium savianum (Caruel) Ball ex Arcang. is a species belonging to Brassicaceae family, that occurs only in Northern Spain and in a few regions of Central Italy, namely Tuscany, Umbria and Latium (Gigante et al. 2014). It is a small annual species with erect habit, branched stems at the base, and an average height between 3 and 10 cm (Pignatti 1982). The genus *Ionopsidium* Rchb., which includes nine recognized species, constitutes the western Mediterranean clade (opposite to the central and northern European/arctic clade of *Cochlearia* L.) of the tribe *Cochlearieae*, a well-defined monophyletic lineage of Brassicaceae. These two genera resulted from a deep evolutionary split dating to the middle Miocene and separating the tribe into two clades with very different evolutionary dynamics (Kock et al. 2012). In Italy, *I. savianum* is categorized as Least Concern according to IUCN standards (Gigante et al. 2014). Moreover, it is considered a species worthy of conservation in the European Community, being included in the Habitats Directive 92/43/CEE, Annexes I and II, and according to the Geneva Convention. This species can be found on different substrates, as it grows mainly on limestone substrates but also on ultramafic outcrops (Gigante et al. 2014). In these different contexts it can be found predominantly in open communities like mead-

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ows, mountain and hill grasslands, path edges and edges of Mediterranean scrub vegetation, between 300 and 1.600 meters a.s.l.

Important hints to help fill the picture of relationships among species in a community can be offered by the evaluation of phylogenetic diversity. Indeed, the use of molecular phylogenies may help analyze the forces that influence patterns of biodiversity and biogeography, and in depicting the interactions among co-occurring species (Selvi et al. 2016). Especially when supported by data on functional diversity, phylogenetic information can be used in the study of the phylogenetic overdispersion or clustering of the community in relation to the variation of the habitat conditions (Erickson et al. 2014, Qian and Jiang 2014, Selvi et al. 2016, Mugnai et al. 2022).

Moreover, considering that soil type is one of the most important ecological factors for plant communities' evolution and development, and is often pivotal in plant species diversification (Rajakaruna 2018), we compared the structure and functional profile of the communities hosting this species on limestone and serpentine. Particularly to the latter, it should be noted that serpentine outcrops are chemically extreme substrates, extraordinarily challenging for plant life (Lefèbvre and Vernet 1990). They are characterised by a multifaceted source of stress, linked to high concentrations of trace elements (namely Ni, Co, and Cr), along with other edaphic constraints, including high Mg concentration, low Ca/Mg ratio, high pH values, and heat stress (Brooks 1987; Gonnelli and Renella 2012; Kazakou et al. 2008; Rajakaruna and Boyd 2009). While taxonomic features are generally used to provide a description of plant communities, it is widely recognised that much more information can be evaluated by adopting a multifaceted approach, including functional traits (Garnier et al. 2004, Chase et al. 2019). In this sense, functional traits and their universal approach may inform on ecosystem multifunctionality and services, also providing insights into the plant communities' direct response, often easily interpretable, to environmental changes (Violle et al. 2007, 2014). Accordingly, trait-based metrics may be used together with taxonomic ones, as they may better depict biodiversity patterns across different spatial scales (de Bello et al. 2013, Mugnai et al. 2022), and for this reason, trait-based studies have become extremely common in plant ecology (Chelli et al. 2019). Despite this, through the review of trait-based ecological studies performed in Italy (Chelli et al. 2019), some gaps have been highlighted, such as the Mediterranean ecosystems are still poorly represented (e.g., Bricca et al. 2020, Stanisci et al. 2020, Mugnai et al. 2021). Moreover, Pierce et al. (2016) recently showed that the measurement of only three leaf functional traits: leaf area (LA), leaf dry matter content (LDMC) and specific leaf area (SLA), may be useful to assess the position of individuals in the framework of Grime's Competitive Stress-tolerant Ruderal (CSR) theory (Grime 1977, Grime and Pierce 2012).

In this study, we aimed at examining differences in taxonomic, phylogenetic and functional diversity of plant communities hosting *I. savianum* in two distant areas with limestone and serpentine substrates. This information is helpful in filling important gaps in the knowledge of the ecology of *I. savianum*, considering that specific studies on communities where the species grows are lacking and only phytosociological information can be usually found (Gigante et al. 2014). Particularly we expected a polarization of the communities of serpentine sites towards the Stress-tolerant strategy, and this should be reflected in the functional traits of the plant in the communities, based on the premises expresses above on the harsh conditions linked to the serpentine substrate. Moreover, we aimed to assess whether local micro-site conditions may affect the different facets of diversity in addition or in contrast to soil type.

Methods

Study area and sampling design

In Tuscany, *Ionopsidium savianum* has only been reported in three locations: Mt. Calvi, Mt. Pelato, and Mt. Carvoli (Gigante et al. 2014) while its presence was excluded in inner areas of Tuscany (Bonari et al. 2016). For the purposes of our study, we selected two localities where this species is relatively abundant and growing on limestone, Mt. Calvi (43.094514° N, 10.624628° E) and serpentine, Mt. Pelato (43.435280° N, 10.430432° E) (Fig. 1). At both the sites *I. savianum* inhabits open areas, i.e. stony grasslands.

Mt. Calvi is located in Campiglia Marittima municipality. It has a maximum elevation of 646 meters a.s.l. The site is characterized by limestone on top (where *I. savianum* grows) and granite in the lower part of the hill. The vegetation is represented mostly by a mixed broadleaved forest, with holm oak (*Quercus ilex*) and deciduous oaks (mostly *Q. pubescens*), but the higher portion of the mountain is characterized by open grassland mostly referable to the class *Festuco-Brometea*, with very sparse cover of shrubs (mostly *Quercus* spp.) and some degree of pastoral activities (sheep grazing). The slopes of the site are subjected to intense mining activities. The area is comprised within the Special Areas of Conservation "Monte Calvi di Campiglia" (SCI/SAC IT5160008).

Mt. Pelato is located in the municipality of Rosignano Marittimo and consist in a low hill (378 meters a.s.l.) close to the Tyrrhenian Sea mainly formed by serpentine rocks. Together with the typical Mediterranean climate, this strongly determines its vegetation which mostly consists of Mediterranean sclerophyllous shrublands. The hilltop and the south-facing slopes are characterized by a stunt and open garrigue-like vegetation, highly adapted to the rocky ultramafic soil.

Sampling design

A census of all the individuals of *Ionopsidium savianum* was carried out in both the study areas in March 2019, recording with a GPS device the position of all detectable plant clusters distant at least 3 meters from each other. Subsequently, among all GPS points, we randomly selected 10 points (at least 10 meters apart) in each study area (total of 20 sampling points) for the survey of the plant communities, completed in the subsequent days (mid-April 2019). Plant names are according to the Portal to the Flora of Italy vers. 2021.2 (http://dryades.units.it/floritaly/), while the syntaxa names follow The Italian Vegetation Prodrome (Biondi and Blasi 2015).

Each point was used to place (on the North-Western corner) a ready-made 1 × 1 m quadrat frame (Fig. 1), in which we surveyed the plant communities hosting *I. savianum* by estimating the percentage of ground cover of each plant species. Following Dengler et al. (2016), we also collected environmental information such as slope aspect, inclination and microrelief (calculated by first placing on the ground a straight stick and then measuring the maximum perpendicular distance from the stick to the ground in the most rugged part of the plot). The slope aspect was transformed into northerness according to the formula: northerness = cosine [(aspect in degrees * π)/180)].

Traits measurement

To assess the functional features and the adaptive strategy of sampled communities, we measured a specific set of traits of species constituting 80% of the total coverage of each plot (Pérez-Harguindeguy et al. 2013), leading to the sampling of 32 species. The measurements and collection of sampled individuals followed the indications detailed in Pérez-Harguindeguy et al. (2013). For each species, we selected five individuals, for which we collected: a) plant height (measured before the specimen collection, in cm); b) leaf fresh weight (LFW); c) leaf area (LA), calculated after digitizing the leaf outline (1200 dpi) using ImageJ v. 1.51 software (Schneider et al. 2012) in mm^2 and d) leaf dry weight (LDW), after 72 h at 70 °C in an oven. The measurement of leaf traits was conducted on five leaves per individual, which were immediately immersed in cool deionized water and processed within 24 hours from collection. Leaf weight was measured with an analytical balance, accurate to 0.02 mg. For each leaf, we further calculated SLA and LDMC according to Pérez-Harguindeguy et al. (2013).

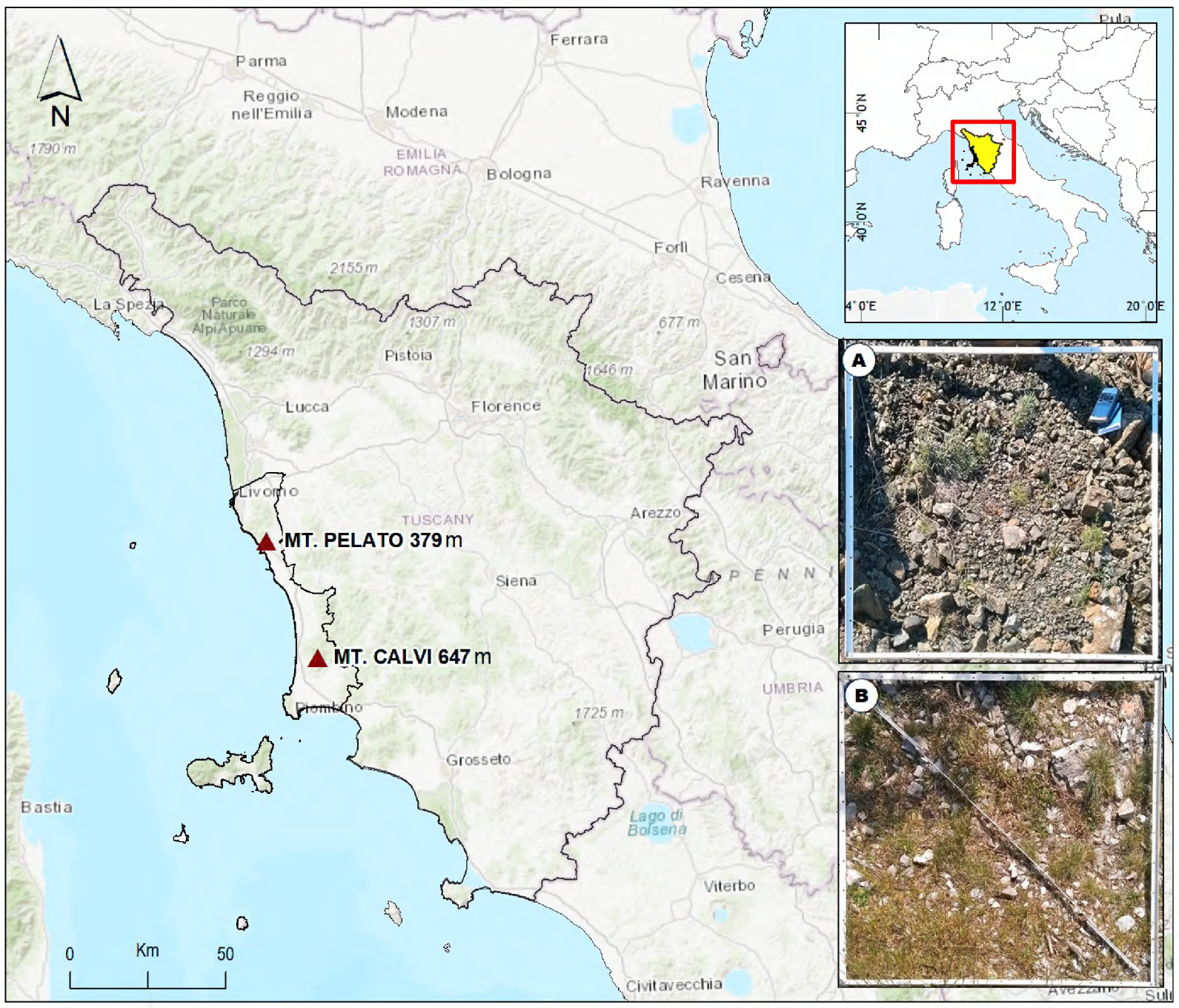

Figure 1. Location of the two study areas (Mt. Pelato and Mt. Calvi in Tuscany, Italy). Pictures of sampling points of 1×1 meter side at A) Mt. Pelato and B) Mt. Calvi. Map source: ESRI (2022).

Calculation of diversity indices

The taxonomic diversity of plant communities was evaluated as species richness (SR) and species diversity (expressed as Shannon H').

A phylogenetic tree of the sampled communities was built from the megaphylogeny of vascular plants (PhytoPhylo) in Qian and Jin (2016), using the R package V. PhyloMaker (Jin and Qian 2019). The PhytoPhylo megaphylogeny was developed from the largely used phylogeny developed by (Zanne et al. 2014) and allows to generate phylogenies robust for studies of community ecology and biogeography, particularly those seeking for patterns of phylogenetic properties along environmental gradients (Qian and Jin 2016). Using this phylogenetic tree, we calculated three indices to explore different features of phylogenetic diversity. We calculated the phylogenetic diversity (PD) as a measure of the amount of phylogenetic richness in the communities (how much) and the mean nearest taxon distance (MNTD) for taxa in a community and the mean pairwise distance separating taxa in a community (MPD) to provide information regarding the phylogenetic divergence within the communities (how different they are; see Tucker et al. 2016). MNTD describes the phylogenetic relatedness among species, focusing on the distal part of the tree, thus involving lower taxonomic levels (Webb et al. 2002). MPD is a measure of the relationship at the higher-level groups in the phylogenetic tree (Webb 2000). For all three indices, we used their standardized effect size relatives (PD.SES, MPD.SES and MNTD.SES, respectively), which are considered less sensitive to species richness (Pavoine et al. 2013) and indicate whether the observed index is different from what would be expected by chance. Positive values of PD.SES indicate that phylogenetic diversity is higher than expected considering the taxonomic species richness. Positive values of MPD.SES and MNTD.SES indicate that observed phylogenetic distances are higher than expected and that phylogenetic overdispersion or evenness occurs, while negative values of such indices indicate phylogenetic clustering. All standardized effect size indices were calculated using a comparison with *fixed-fixed* null models, which maintain both species richness and species abundance across sites and tend to exhibit low type I and II error rates (Miller et al. 2016). The null model matrices were randomized using the "independent-swap" algorithm by Gotelli (2000).

Functional diversity at the plot level was evaluated using Rao's quadratic entropy (de Bello et al. 2010), which represents a measure of species traits' dissimilarities and equals the sum of the dissimilarity in trait space among all possible pairs of species, weighted by the product of the species relative abundance. For each trait (i.e. LA, LDMC, SLA, H), we also provide the community-weighted mean values (hereafter CWM; Garnier et al. 2004) based on the relevant species' cover within the plot. CWM reflects the dominant trait values and is often used to quantify shifts in such values along different environmental conditions (Garnier et al. 2004, Ricotta and Moretti 2011).

To calculate the relative contribution of CSR parameters for each species we used the *StrateFy* analysis tool, which allows calculating the CSR coordinates of the species using the values of LA, SLA and LDMC (Pierce et al. 2016). Again, CWM was also adopted to calculate the dominant CSR strategies within each plot, to provide a measure of the dominant strategies characterizing the communities. Subsequently, these values were used as coordinates to display the community dominant strategy in the ternary CSR diagram of Grime.

Data Analyses

To assess the compositional features of the sampled communities we performed a canonical correspondences analysis (CCA) on the specie per plot matrix (i.e. 97 species × 20 plots). Species cover values were arc-sine transformed. Site, northerness and microrelief were used as explanatory variables and the significance of the constrained axes was tested with 4,999 unrestricted permutations and summarized by adopting the false discovery rate (Benjamini 2010). To further evaluate the compositional differences between the two communities, we carried out an Indicator Species Analysis (ISA) following Dufrêne and Legendre (1997). The ISA allows computing an indicator value *d* (ranging between 0 and 100) of each species as the product of the relative frequency and relative average abundance of species in clusters. The analysis also produced a significance value, representing the probability of obtaining a *d* value as high as that observed over 1000 iterations. We conducted the analyses considering the two sites as separate clusters.

The effect of site and local-plot conditions on total plant cover, taxonomic, phylogenetic and functional diversity, as well as on the CMW-adaptive strategy, was studied by fitting a series of models with site, northerness, microrelief and their interaction terms used as predictors. To avoid model overfitting (given our low number of replicates) we used the framework of multi-model inference through the Information-Theoretic Approach (Burnham and Anderson 2002) to evaluate the importance of predictors and to select a set of "best models". Model comparisons were performed using the corrected Akaike Information Criterion (AICc). According to this procedure, we estimated the relative importance $w_{r(j)}$ of each predictor *j* as the sum of the AICc weights across all models in which the selected predictor appeared. Predictors with higher $w_{r(j)}$ have a higher weight of evidence to explain the response variable with the given data (i.e. strong explanatory variable will have a $w_{r(j)} > 0.9$, moderate effects $w_{r(j)} > 0.7$; for interactions, a strong effect will be $w_{r(j)} > 0.7$, moderate wr(j) > 0.5). From all the possible models we selected all the models with a ΔAICc < 4 (which represents the difference between each model and the most parsimonious one). The correlation coefficients of selected predictors were averaged among the selected best-fitting models and the significance of the estimated coefficient was calculated

with a *z*-test. To enhance model fitting and comparability among coefficients, countable variables were centered and scaled for the model fitting, and back-transformed for the plotting of the fitted relationships.

The CCA has been run using the software Canoco 5 vers. 5.15 (ter Braak and Smilauer 2012). All other analyses were run in R vers. 4.1.3 (R Core Team 2021), and relative graphs were produced with the packages *cowplot* vers. 1.1.1 (Wilke 2022), *ggtern* vers. 3.3.5 (Hamilton and Ferry 2018), *ggplot2* vers. 3.3.6 (Wickham 2016). The ISA was conducted using the package *labdsv* (Roberts 2022). The multi-model comparisons and inference were performed using the *MuMIn* package vers. 1.46.0 (Bartoń 2022).

Results

The sampling resulted in 97 species (Suppl. Material 1, Table S1), with 14 shared species among the two habitats, 57 species exclusive of Mt. Calvi and 26 of Mt. Pelato. Plot-level environmental variables sampled or calculated are shown in Suppl. Material 2, Table S2.

According to the CCA, the species composition of plots resulted largely different among the two sites (p-value < 0.001, variance explained 17.5%, see Fig. 2), and also significantly influenced by northerness (p-value = 0.039, variance explained = 6.6%). Conversely, the effect of microrelief was not significant. The total variance was 4.51 and explanatory variables accounted for 29%. Axis 1 was linked to site, while the effect of northerness and microrelief (which appeared correlated) lay on Axis 2 (Fig. 2). The ISA (Table 1) confirmed a high differentiation among the plant communities at the two sites, with Mt. Calvi showing a higher number of indicators species than Mt. Pelato (14 and 9 significant indicator species, respectively).

The indices of taxonomic diversity were all significantly affected by the Site (which showed significant coefficients and generally high importance scores), but not by the plot-level conditions (Table 2). All the indices, i.e. species richness, total plant cover on the plot and species diversity expressed as Shannon H' index, were higher at Mt. Calvi (Fig. 3).

All the indices of phylogenetic diversity resulted influenced by site and microrelief. Indeed, the effect of the latter changed among the two different sites (in all cases the interaction term site:microrelief was highly significant and with high importance scores; Table 3). At Mt. Pelato all phylogenetic diversity indices increased drastically as the plot's microrelief values increase, while almost no effect was detected for Mt. Calvi (Fig. 4).

Functional diversity expressed as Rao's quadratic entropy was significantly different among the two sites (the term site was highly significant and showed a very high importance score; Table 4), and resulted higher at Mt. Pelato (Fig. 5A). Among the leaf functional traits, only SLA varied significantly among the two sites, with an interaction effect with northerness (p-value = 0.049; Table 4), although site was by far the more important term.

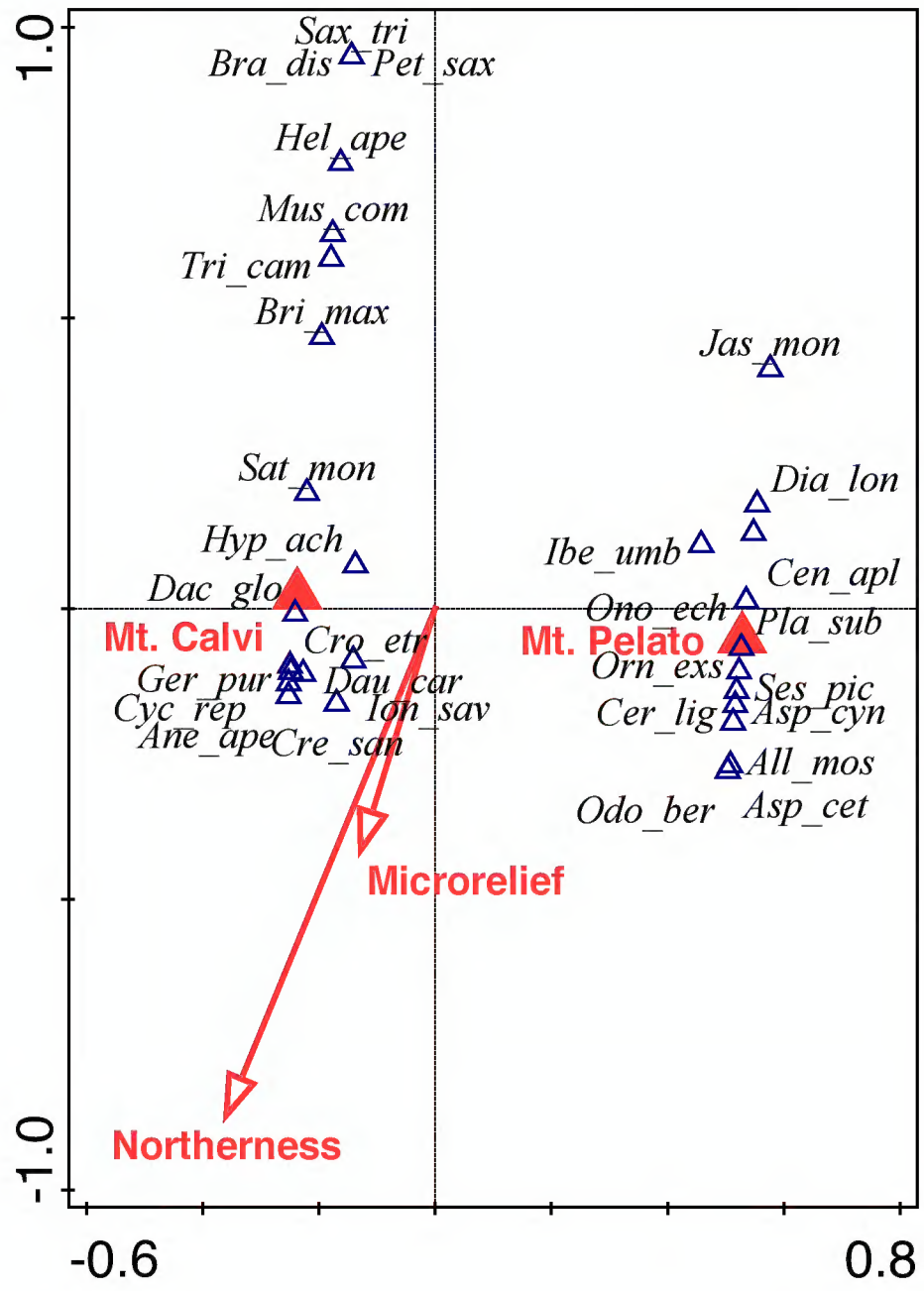

Figure 2. Canonical correspondences analysis (CCA) ordination plot based on species composition of the communities at Mt. Calvi and Mt. Pelato. Site, northerness and microrelief are used as explanatory variables. Blue empty triangles represent the species, while filled red triangles represent plot centroids according to the site. Only 30 best-fitting species are shown (the first 30 species showing the highest correlation with the first CCA axis). See Suppl. Material 2, Table S2 for species names abbreviations.

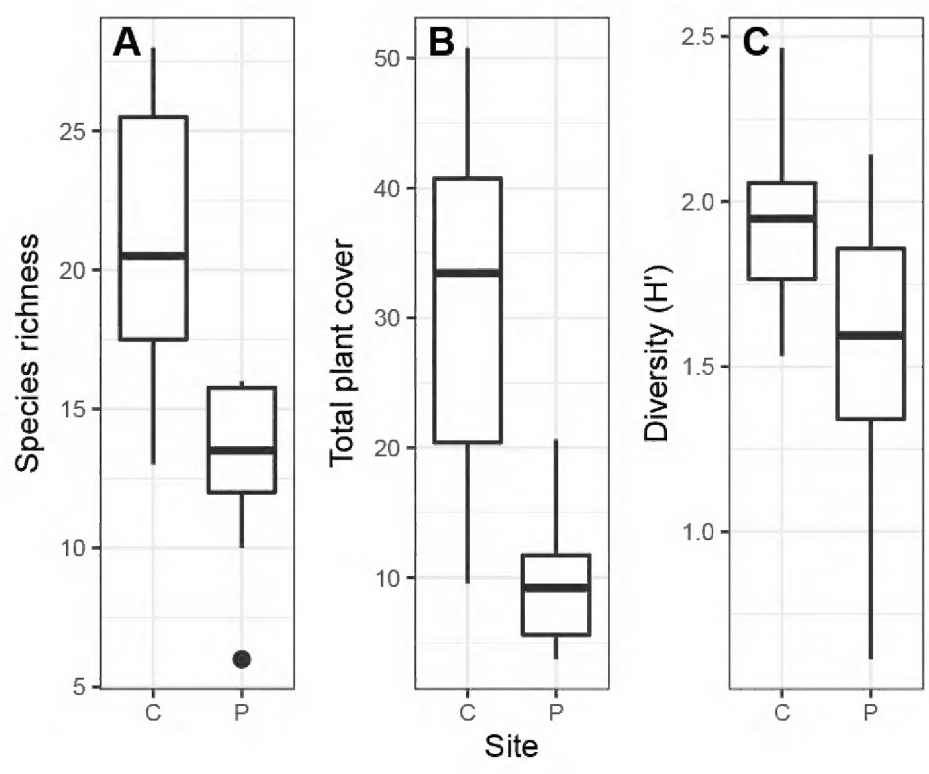

Figure 3. Effect of the site on A) Species richness, B) Total plant cover and C) species diversity expressed as Shannon H' index. Sites: C = Mt. Calvi, P = Mt. Pelato.

Table 1. Results of indicator species analysis of plant species through comparison of the two study areas (Mt. Pelato and Mt. Calvi). Only species showing significant indicator values (P-value <0.05) are shown.

Species	Indicator value	P-value
	Mt. Calvi	
Ionopsidium savianum	0.97	0.004
Dactylis glomerata	0.90	0.001
Geranium purpureum	0.90	0.001
Daucus carota	0.90	0.002
Hypochaeris achyrophorus	0.87	0.006
Cerastium glomeratum	0.68	0.046
Anemone apennina	0.60	0.007
Anisantha madritensis	0.60	0.024
Crepis sancta	0.57	0.043
Crupina crupinastrum	0.50	0.029
Lysimachia linum.stellatum	0.50	0.029
Satureja montana	0.50	0.037
Sherardia arvensis	0.50	0.030
Viola arvensis	0.50	0.028
	Mt. Pelato	
Centaurea aplolepa	0.80	0.001
Cerastium ligusticum	0.80	0.002
Ornithogalum exscapum	0.80	0.001
Sesleria pichiana	0.80	0.001
Iberis umbellata	0.73	0.005
Onosma echioides	0.70	0.006
Plantago subulata	0.60	0.011
Allium moschatum	0.50	0.040
Odontarrhena bertolonii	0.50	0.023

Table 2. Results for the multimodel inference on the role of site, northerness and microrelief in explaining the variation in total plant cover and taxonomic diversity of the monitored plots. Averaged coefficient and relative importance for each environmental predictor are given for the best linear models (AICc < 4). Significance codes: P-value < .001 '***'; P-value < .01 '**'; P-value < .05 '*'.

Response variable	Term	Relative Importance	Estimate	Adjusted SE	z-value	P-value	
Total plant cover	(Intercept)	-	0.72	0.23	3.05	0.002	**
	Site	1.00	-1.43	0.33	4.28	<0.001	***
	Northerness	0.31	0.17	0.17	0.98	0.327	
	Microrelief	0.22	0.09	0.17	0.53	0.594	
Species richness	(Intercept)	-	0.65	0.24	2.65	0.008	***
	Northerness	0.59	0.31	0.20	1.58	0.115	
	Site	0.99	-1.30	0.35	3.71	<0.001	***
	Microrelief	0.29	0.14	0.18	0.77	0.440	
	Northerness:Site	0.10	-0.23	0.36	0.64	0.520	
Diversity (H')	(Intercept)	-	0.33	0.35	0.93	0.351	
	Site	0.74	-0.90	0.44	2.07	0.039	*
	Northerness	0.41	0.31	0.23	1.31	0.190	
	Microrelief	0.35	0.26	0.22	1.14	0.255	

Table 3. Results for the multimodel inference on the role of site, northerness and microrelief in explaining the variation in phylogenetic diversity of the monitored plots. Averaged coefficient and relative importance for each environmental predictor are given for the best linear models (AICc < 4). PD.ses = standardized effect size of phylogenetic diversity, MNTD.ses = standardized effect size of mean nearest taxon distance, MPD.ses = standardized effect size of mean pairwise distance. Significance codes: P-value < .001 '***'; P-value < .01 '**'; P-value < .05 '*'.

Response variable	Term	Relative Importance	Estimate	Adjusted SE	z-value	P-value	
PD.ses	(Intercept)	-	-0.19	0.28	0.68	0.496	
	Microrelief	0.81	-0.22	0.21	1.04	0.298	
	Site	0.79	0.54	0.38	1.41	0.158	
	Microrelief:Site	0.74	1.78	0.53	3.34	<0.001	***
MNTD.ses	(Intercept)	-	0.02	0.27	0.08	0.936	
	Microrelief	0.74	-0.47	0.22	2.16	0.031	*
	Site	0.72	0.05	0.39	0.12	0.906	
	Microrelief:Site	0.65	1.78	0.55	3.27	0.001	**
MPD.ses*	(Intercept)	-	-0.48	0.20	-2.39	0.030	*
	Microrelief	1.00	-0.04	0.16	-0.27	0.788	
	Site	0.99	1.05	0.28	3.71	0.002	**
	Microrelief:Site	0.98	1.68	0.40	4.24	<0.001	***

Generally, SLA was smaller at Mt. Pelato, where no significant changes were recorded due to northerness, while at Mt. Calvi SLA appeared greater, and increased with the northerness (Fig. 5B). Plant height within communities was affected by northerness (p-value = 0.046; Table 4), indeed at both sites, it increased with the north exposition (Fig. 5C). Looking at the CSR adaptive strategies coordinates (Fig. 5D), both communities showed low participation of competitive species (Mean CWM C component: Mt. Calvi 13.31%, Mt. Pelato 10.12%), being dominated by stress-tolerant species (Mean CWM S component: Mt. Calvi 49.58%, Mt. Pelato 82.29%), but with an important contribution of ruderal species at Mt. Calvi (Mean CWM R component: Mt. Calvi 37.11%, Mt. Pelato 7.6%). The two communities were quite differentiated as to S- and R-strategies, and resulted both influenced by an interaction effect of northerness and site (p-value = 0.014 in both cases, see Table 4). In general, Mt. Pelato was characterized by a high contribution of the S strategy irrespective of slope aspect (no variation with northerness), while at Mt. Calvi the importance of the S strategy decreased at increasing northerness, with R-strategy importance increasing (Figs 5E and F).

Discussion

Within this contribution, we aimed at analyzing the taxonomic, phylogenetic and functional features of two diverse plant communities hosting *Ionopsidium savianum*, growing at two important sites of occurrence of this species in Tuscany, with very different soil types: limestone (Mt. Calvi) and serpentine rocks (Mt. Pelato). The two communities investigated resulted to be different from multiple points of view.

Firstly, they differed taxonomically in terms of species composition, species richness, total cover and Shannon diversity, with Mt. Pelato showing lower values for all these indices. Such differentiation appears mainly explained by the different types of substrate in the two sites. Indeed, the substrate can affect substantially also the same vegetation types, like in the case of species-rich *Nardus stricta* grasslands hosting a higher vascular plant diversity on calcareous than on siliceous bedrock (Pittarello et al. 2017). This differentiation appears greater considering the specifity of the vegetation growing on serpentine substrate. Indeed, it should be noted, that even if from a structural and physiognomic point of view the two communities that we analyzed are somehow similar (i.e. open garrigues/grasslands with sparse shrublets and abundant rockiness), they are quite different from the phytocoenological point of view. In both areas annuals (*Tuberarietea guttati* class), succulents (*Sedo-Schleranthetea* class) and semi-mesophilous grasses and herbs (*Festuco-Brometea* class) are present, but Mt. Calvi communities are rich in small chamephytes such as *Satureja montana* and *Helianthemum apenninum*, typical of some Apennine hilly and montane garrigues (mainly attributable to *Artemisio albae-Brometalia erecti* suborder, but see also Mucina et al. 2016 and Terzi et al. 2016), recently also proposed as a new habitat of conservation importance (Casavecchia et al. 2021), while in Mt. Pelato's coenoses the relevant species are those typical of serpentine substrates (which resulted also as indicator species for Mt. Pelato), either strictly endemic or preferential, such as *Odontarrhena bertolonii*, *Centaurea aplolepa* subsp. *maremmana*, *Sesleria pichiana*, *Plantago subulata*, *Iberis umbellata*, *Onosma echioides* (mainly attributable to *Alyssion bertolonii* alliance); also these communities are important as a habitat of conservation relevance according to the Habitats Di-

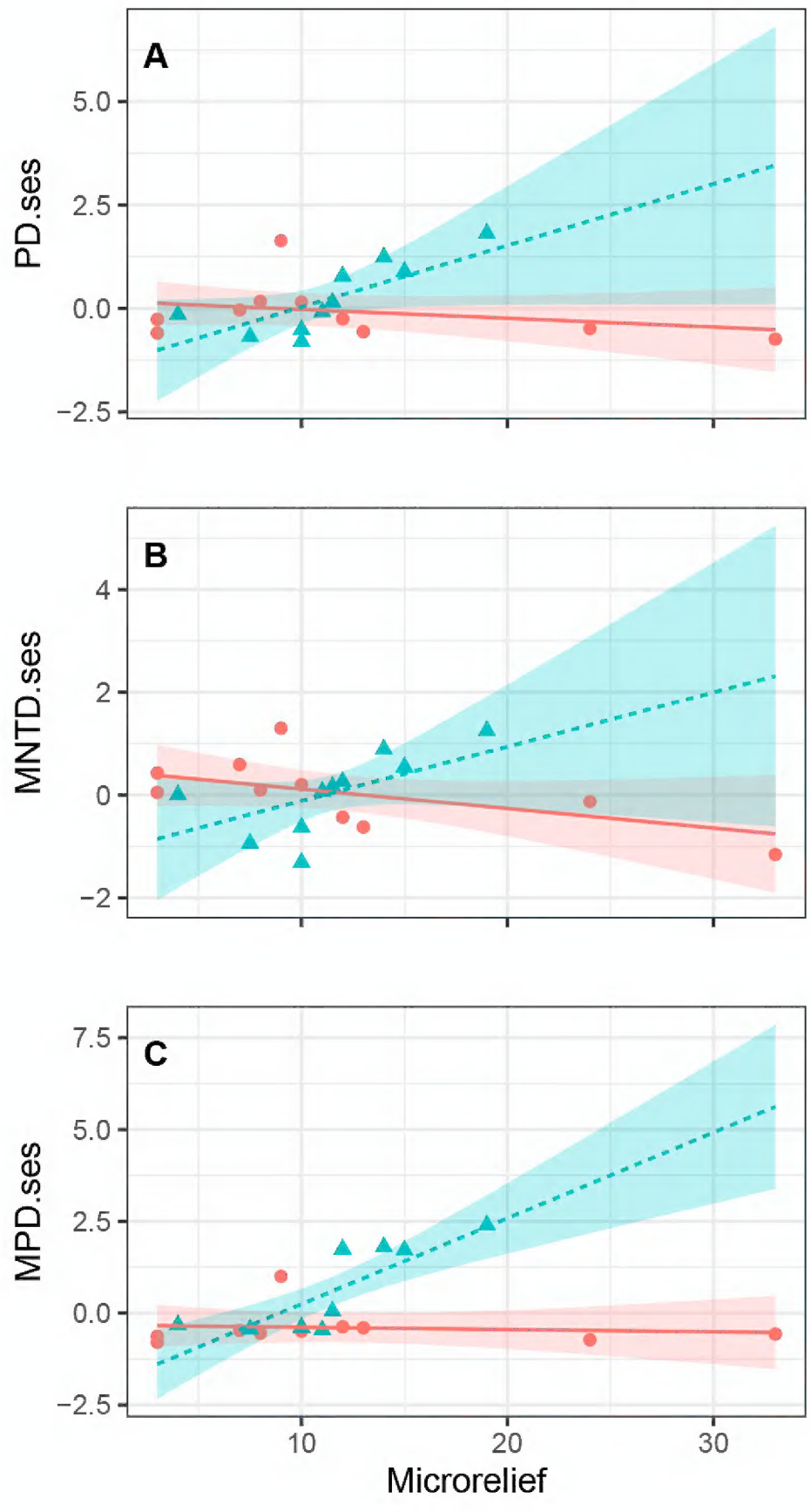

Figure 4. Effect of site and microrelief on the indices of phylogenetic diversity. A) standardized effect size of phylogenetic diversity (PD.ses); B) standardized effect size of mean nearest taxon distance (MNTD.ses); C) standardized effect size of mean pairwise distance (MPD.ses). Sites: red circles = Mt. Calvi, blue triangles = Mt. Pelato.

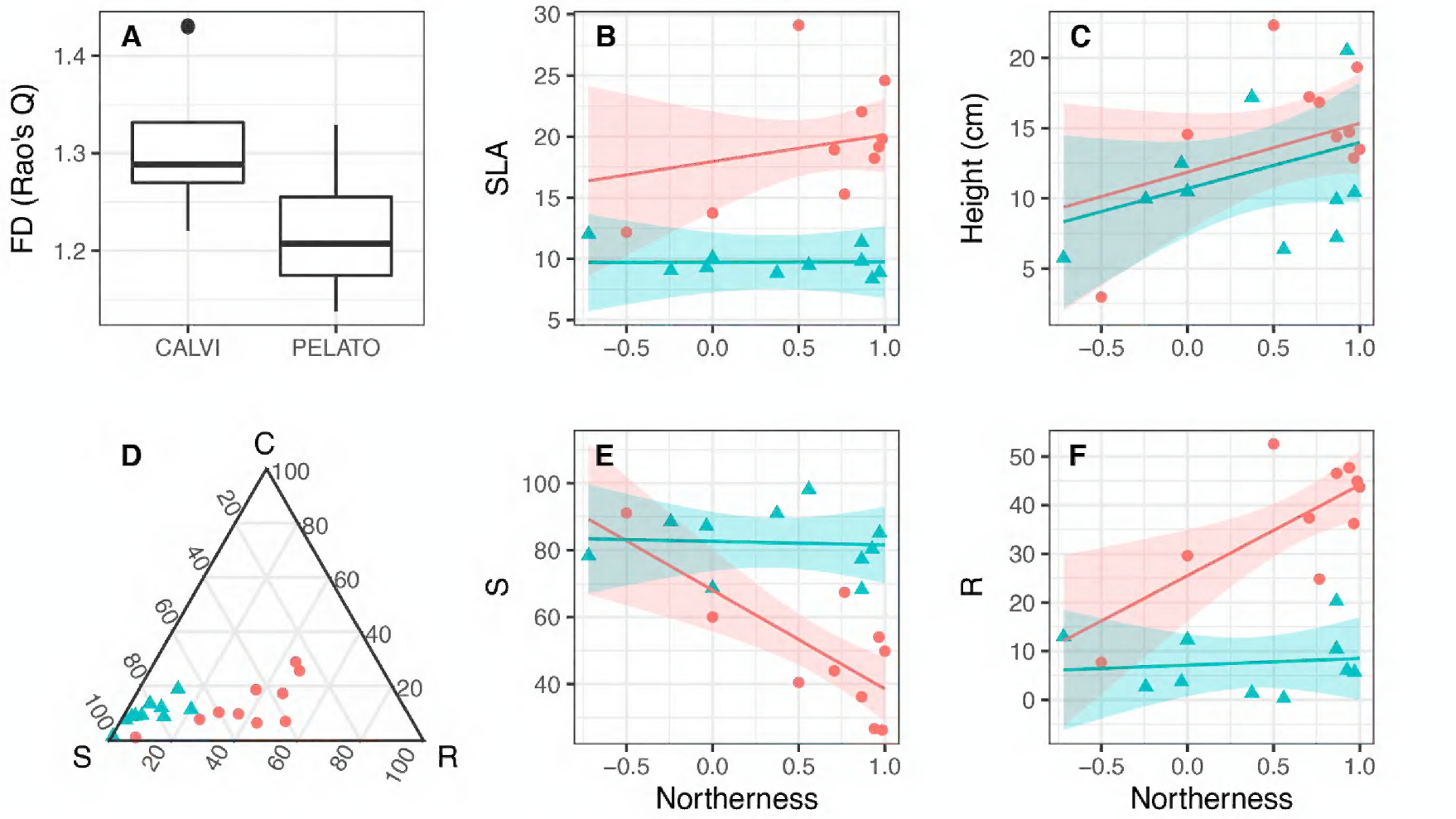

Figure 5. A) Functional diversity expressed as Rao's quadratic entropy in function of site. B-F) Community weighted mean for the tested traits B) Specific leaf area (mm2/mg) and C) Plant mean height in function of site and northerness, D) Ternary diagram reporting the Grime's Competitive Stress-tolerant Ruderal (CSR) adaptive ecological strategies at the plot level, E) Stress-tolerant and F) Ruderal strategy in function of site and northerness. Sites: red circles = Mt. Calvi, blue triangles = Mt. Pelato.

rective (Biondi and Blasi 2015, Casavecchia et al. 2021). These communities showed a lower taxonomic diversity, probably due to the harshness of the environmental conditions typical of the serpentine substrate. Indeed, already Selvi (2007) found for the serpentine flora of Tuscany a relatively low species diversity, but a considerable taxonomic distinctiveness, resulting from the selective pressure of serpentine soils.

Interestingly, microrelief resulted as the only factor shaping the phylogenetic structure of communities, though in a different way in the two sites. While at Mt. Calvi there was almost no variation in the indices of phylogenetic diversity, at Mt. Pelato there was in all three indices a significant positive correlation with microrelief. This pattern may be the result of the occurrence of particular ecological conditions linked to more rugged soils (i.e. with higher microrelief), which allows the establishment of different phylogenetic groups. Indeed, the two sites with higher microrelief at Mt. Pelato are the only ones hosting a fern (*Asplenium ceterach* L.). It has already been shown that the presence of a single species characterized by a deep separation in the phylogeny of the communities may raise substantial differences in phylogenetic trends (Lazzaro et al. 2020).

Finally, the two communities showed significant differences in the level of functional diversity and displayed a differentiation in terms of leaf traits and dominant CSR strategy. Noteworthy, the higher mean species richness detected at Mt. Calvi was paralleled by a higher functional diversity. This is consistent with studies on the relationship between species diversity and functional diversity, which generally predict that increasing species diversity results in increasing functional diversity (Biswas and Mallik 2011). Moreover, the lower functional diversity retrieved at Mt. Pelato may be explained by a stronger environmental filter acting on plant communities (Götzenberger et al. 2012). In this case, the harsh soil conditions (low water availability and heavy metals abundance) represent a strong environmental filter which led to strong functional adaptation to survive in such an environment (i.e., lower SLA; see Kandlikar et al. 2022). Conversely, the more favorable conditions of Mt. Calvi, in terms of resources availability and soil composition, result in weaker environmental filters on communities and allow the coexistence of multiple adaptations to survive and reproduce, determining a higher functional diversity (de Bello et al. 2013).

The higher SLA detected on Mt. Calvi, may be linked to the higher abundances in this site of species with a resource-acquisition strategy, which usually show high growth rates and photosynthetic efficiency (Wright et al. 2004). On the other hand, plant size (i.e. in our case plant height) was mainly linked in both sites to the plot aspect. The importance of the slope aspect on vegetation is well known (see for instance the effect of the slope aspect on Mediterranean vegetation in Kutiel 1992, Sternberg and Shoshany 2001). In our case, it is conceivable that the northern expositions buffer aridity and sun exposure in both sites, allowing the establishment of bigger plants and fostering their dominance within the communities. Moreover, it has been recently shown that Mediterranean

Table 4. Results for the multimodel inference on the role of site, northerness and microrelief in explaining the variation in functional diversity of the monitored plots. Averaged coefficient and relative importance for each environmental predictor are given for the best linear models (AICc < 4). Significance codes: P-value < .001 '***'; P-value < .01 '**'; P-value < .05 '*'.

Response variable	Term	Relative importance	Estimate	Adjusted SE	z-value	P-Value	
Rao's quadratic entropy	(Intercept)	-	0.55	0.28	1.95	0.051	.
	Site	0.93	-1.11	0.40	2.75	0.006	**
	Northerness	0.30	0.20	0.21	0.96	0.337	
	Microrelief	0.37	0.25	0.22	1.17	0.244	
	Microrelief:Site	0.10	-0.68	0.55	1.24	0.216	
Leaf area	(Intercept)	-	0.05	0.27	0.17	0.867	
	Microrelief	0.67	0.43	0.22	1.91	0.057	.
	Northerness	0.48	0.43	0.33	1.29	0.198	
	Site	0.35	-0.36	0.45	0.80	0.424	
	Northerness:Site	0.11	-0.88	0.46	1.91	0.056	.
Leaf dry matter content	(Intercept)	-	-0.01	0.26	0.05	0.959	
	Microrelief	0.37	-0.28	0.24	1.14	0.256	
	Northerness	0.30	0.20	0.25	0.80	0.421	
	Site	0.22	0.22	0.49	0.45	0.652	
Specific leaf area	(Intercept)	-	0.74	0.21	3.54	<0.001	***
	Site	1.00	-1.53	0.29	5.27	<0.001	***
	Northerness	0.55	0.38	0.25	1.52	0.129	
	Northerness:Site	0.36	-0.56	0.28	1.97	0.049	*
	Microrelief	0.17	0.01	0.15	0.06	0.953	
Plant height	(Intercept)	-	0.12	0.30	0.40	0.688	
	Northerness	0.78	0.48	0.24	2.00	0.046	*
	Site	0.46	-0.60	0.45	1.33	0.184	
	Microrelief	0.23	0.02	0.23	0.11	0.914	
	Northerness:Site	0.06	-0.37	0.46	0.80	0.424	
C	(Intercept)	-	0.04	0.26	0.15	0.883	
	Microrelief	0.62	0.41	0.24	1.71	0.087	.
	Northerness	0.56	0.39	0.26	1.51	0.131	
	Site	0.29	-0.34	0.47	0.73	0.467	
	Microrelief:Northerness	0.05	-0.09	0.48	0.20	0.844	
	Northerness:Site	0.06	-0.75	0.48	1.58	0.114	
S	(Intercept)	-	-0.55	0.19	2.90	0.004	**
	Northerness	1.00	-0.71	0.21	3.37	<0.001	***
	Site	0.94	1.26	0.27	4.74	<0.001	***
	Northerness:Site	0.80	0.69	0.28	2.46	0.014	*
	Microrelief	0.40	-0.17	0.13	1.30	0.194	
R	(Intercept)	-	0.67	0.17	4.07	<0.001	***
	Northerness	0.93	0.56	0.20	2.74	0.006	**
	Site	1.00	-1.47	0.23	6.38	< 0.001	***
	Northerness:Site	0.79	-0.58	0.24	2.46	0.014	*
	Microrelief	0.21	0.08	0.12	0.70	0.485	

serpentine communities on northern-facing slopes display reduced plant mortality after extreme heat events (Coppi et al. 2022). Regarding the dominant CSR adaptive strategies, as expected, the Mt. Pelato communities were polarized towards an S-type ecological strategy. Again, this is in agreement with the harsher environmental conditions at Mt. Pelato, leading to the selection of plants with stress-tolerant functional traits, such as small size, thick leaves, and low stature, which confer slow resource acquisition and low growth rates (Damschen et al. 2012, Fernandez-Going et al. 2012, Rajakaruna 2018 for traits evolution in serpentinophytes, and Lazzaro et al. 2021 for variation at the intraspecific level on *Silene paradoxa* L.). In contrast, the Mount Calvi community presented a trend toward an R-type ecological strategy. This strategy is likely linked to the presence of grazing in the area, which is used as sheep pastureland. Thus, species presented a conservative strategy on serpentine substrata and an exploitative strategy on grazed areas, in agreement with previous studies on the leaf economic spectrum (Adamidis et al. 2014).

In conclusion, our results revealed important differences between the communities analysed, highlighting quite different features in taxonomic, phylogenetic and functional diversity, as well as in the dominant ecological strategies. Our data bring evidence for the capability of this species to be part of communities that can highly differ from the ecological point of view even if are structurally and physiognomically similar. These indications may be useful from a conservation point of view as they indicate the need of maintaining the structure of vegetation, for instance with a recursive disturbance, to allow the presence of this protected species. Nevertheless, further studies, including also non-Tuscan occurrence sites, are needed in order to better depict the ecological preferences of this species, considering that Latium and Umbria sites cover a wider range of biogeographical and ecological conditions.

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Supplementary material 1

Table S1

Authors: Michele Mugnai, Emilio Corti, Andrea Coppi, Daniele Viciani, Lorenzo Lazzaro

Data type: table

Explanation note: Species per plot community matrix, with species in the rows and plot in the columns (percentage cover). "**" mark the species for which functional traits have been measured.

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Link: https://doi.org/10.3897/pls2022592/04.suppl1

Supplementary material 2

Table S2

Authors: Michele Mugnai, Emilio Corti, Andrea Coppi, Daniele Viciani, Lorenzo Lazzaro

Data type: table

Explanation note: Environmental variables of the 20 sampled plots. See main manuscript for a more detailed description of the variables. All values are given at the plot level.

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